

The general size and description point to *Rallina tricolor*, but the species has never been collected in the Louisiades.

A medium-sized kingfisher was seen perched in bright sunlight on a low branch over the river. It was a solid, almost royal, blue with no indication of scaling on the head and the underparts were a rich rufous. When it flew, the only turquoise visible was in the rump. The bill was long, black and sturdy with a conspicuous red strip at the base of the lower mandible, and a white marking on the neck was very obvious. It resembled *Alcedo azurea*, which has not been reported from the Louisiades, except that *azurea* has no turquoise in the rump and neither the literature nor specimens indicate the presence of red at the base of the lower mandible.

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Addresses: Mary LeCroy, Department of Ornithology, American Museum of Natural History, New York, NY 10024, U.S.A. William S. Peckover, 14 Balanda Street, Jindalee, Queensland 4074, Australia.

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A parsimonious phylogenetic tree for the swifts, Apodi, compared with DNA-analysis phylogenies

by Jan Holmgren

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In recent years, new and independent data for evaluating phylogenies in birds have been produced through biochemical and statistical analyses of genetic structures. The techniques used are complex, and room for errors of methodology and ambiguities of interpretation should be admitted (Sarich *et al.* 1989, Lanyon 1992). However, to a substantial extent the new results are consistent with one another, but are sometimes in conflict with traditional views (Bleiweiss *et al.* 1994, Lee *et al.* 1996).

The swifts as a group generally seem to exhibit slow, continuous adaptations for their aerial life, giving the impressions of a morphological conservatism caused by the uniformity of the food niche. The great variability in body size may perhaps be linked with interspecific competition. A great deal of other morphological variation may probably be linked with the intermittent contacts with solid matter in breeding and roosting. Here I present a parsimonious phylogenetic tree

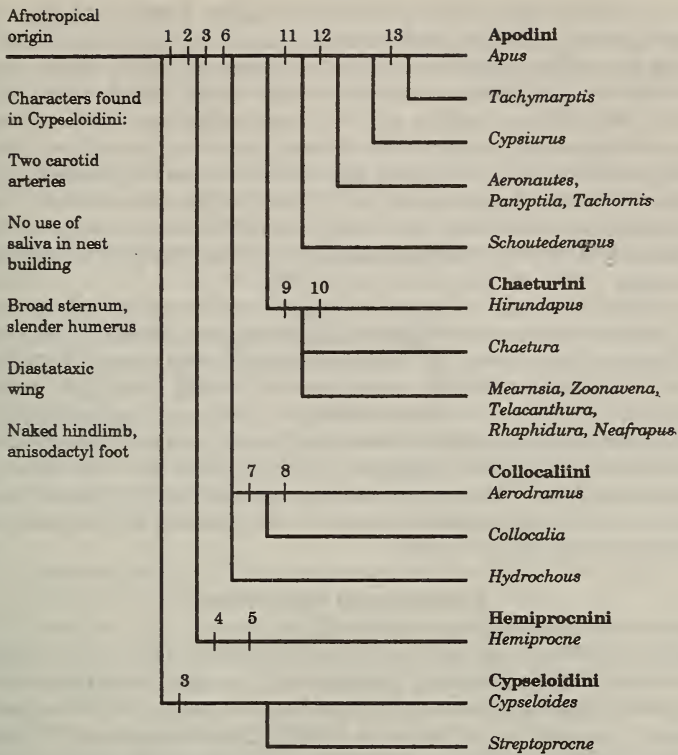


Figure 1. Hypothetical phylogenetic tree for the swifts. No time scale. Numbers denote change of characters as follows: 1. One carotid artery. 2. Use of saliva in nestbuilding. 3. Gradual change towards narrow sternum and stout humerus as adaptations for aerial life. 4. Nesting and roosting on branches, perching. 5. Near stasis (perhaps even regression) in change of sternum and humerus owing to less aerial life. 6. Eutaxic wing. 7. Nesting and roosting in caves, some have feathered hindlimbs. 8. Echolocation. 9. Nesting and roosting inside hollow trees, square and spined tails. 10. No nestbuilding. 11. Feathered hindlimbs. 12. Nesting and roosting in foliage of trees, reduced numbers of phalangi, reversed hindtoe, toes in opposite-pairs. 13. Change to more solid nest and roost sites, tendency towards "all four toes forwards".

for the swifts, which is consistent with a hypothetical historical narrative (Mayr 1988) and zoogeographical facts. This simple tree may serve as a null hypothesis: suggested instances of further convergent or parallel evolution in the specified characters should be explicitly analysed.

Methods

The suggested phylogenetic tree in Figure 1 is derived from key characters (two carotid arteries or one carotid artery (Glenny 1955, Sibley & Ahlquist 1990), no use of saliva or use of saliva in nestbuilding

(Marín & Stiles 1992, Chantler & Driessens 1995), gradual change towards narrow sternum and stout humerus as adaptations for aerial life (Sclater 1865, Harrison 1984), diastataxic (i.e. with apparent absence of 5th secondary remex) or eutaxic wing (Clark 1906, Sibley & Ahlquist 1990)) linked with a general understanding of swift evolution, taking into account the role of various behaviours and substrata in breeding and roosting. A similar approach has proved successful in the swallows (Winkler & Sheldon 1993). The clarification of nest building in the Cypseloidine swifts (Marín & Stiles 1992) is an important recent achievement. The first methodical survey of all swift species (Chantler & Driessens 1995) facilitated an overview.

In any phylogenetic tree, any lineage from the ancestral species to a recent species may be envisaged as a straight continuous line, with all other lineages branching off from that arbitrarily chosen trunk of the tree. In order to standardise trees for the swifts, I suggest that *Apus apus* should be chosen as this favoured recent species, simply because this will produce trees that are most similar to the traditionally accepted order between the main groups of swifts, and so will make direct comparisons easier. Since only the Cypseloidine swifts show primitive states in all the key characters, they are placed at the base of the hypothetical phylogenetic tree.

Results and discussion

The hypothetical phylogenetic tree—Figure 1

Brooke's (1970a) division of the Apodidae into the subfamilies Cypseloidinae and Apodinae (instead of the then traditional division between the Chaeturinae and the Apodinae, based on differences in the hindlimbs, derived from Sclater's (1865) Chaeturinae and Cypselinae) was based on differences in a number of characters. One of Brooke's Cypseloidine characters (diastataxic wing) is also present in the treeswifts, which I now suggest should be placed in Apodinae. Two characters (anisodactylous feet, downlike semiplumes on young nestlings) are present also in some Apodine species. For three characters (egg white profiles with four peaks, little or no transpalatine processes, simple *Musculus splenius capitis*) there is uncertainty about their exact validity, and one character (that there is a sexual dimorphism of plumage in some Cypseloidine species) is questionable since it may be an age character (females acquiring adult plumage later, M. Marín, pers. comm., Chantler & Driessens 1995). However, Brooke's division into subfamilies still seems warranted by two of his characters: the presence of two carotid arteries (Glenny 1955) and the now confirmed (Marín & Stiles 1992) lack of saliva in nest building in the Cypseloidine swifts.

Sibley & Ahlquist (1990) critically reviewed morphological characters used in phylogenetic work. Generally, conditions of the carotid arteries and the 5th secondary were found to be useful to some degree, but not consistent. However, within groups, two carotid arteries and diastataxy were consistently found to represent the ancestral condition. Use of saliva in nest building is special for swifts, and thus represents the derived condition.

The treeswifts have one carotid artery, and they use saliva in nest building. Hypothetically, I suggest that the treeswifts should be treated as a tribe Hemiprocnini within Apodinae, so all extant swifts belong to the family Apodidae. Differences in anatomical details (Lowe 1939) and plumage in the treeswifts may well be explained by their different lifestyle. Fossil and osteological evidence (Sclater 1865, Harrison 1984) show a gradual change of sterna and humeri in the swifts, caused by selection forces linked with their extremely specialised aerial life. A broad sternum and slender humerus in the treeswifts may be explained by near stasis (perhaps even some regression) in this change, following the adoption of a less aerial life.

Analysis of changes in humeral structures led Karkhu (1992) to quite different conclusions, suggesting long independent evolution of the Hemiprocnide and the Apodide swifts. He even suggested that the treeswifts should be placed in a suborder Hemiprocni, while the suborder Apodi would include the other swifts and the hummingbirds, Trochilidae. He did not consider, however, the possibility of near stasis in the treeswifts, coinciding with convergent changes in other lineages leading to recent taxa. His interesting analysis of functional causes for the observed changes may be interpreted in support for convergent change.

The Cypseloidine and Hemiprocnine swifts have diastataxic wings, while all other swifts have eutaxic wings (Clark 1906).

In Collocaliini the Giant Swiftlet *Hydrochous gigas* is remarkably similar to the Cypseloidine swifts, and its choice of nest site is similar (M. Marín, pers. comm., Somadikarta 1968, King 1987). It cannot echolocate, and its nest is similar to Cypseloidine nests, except that some saliva is used (Becking 1971).

When erecting the genus *Schoutedenapus*, De Roo (1968) pointed out a close similarity to *Apus*, but he found it impossible to place the taxon within *Apus* owing to the unmodified (anisodactyl) feet. He discussed, however, the possibility that the feathering of the legs may have been a first step in the evolution of the Apodine foot. Brooke (1970a) temporarily placed *Schoutedenapus* in Collocaliini, and he is followed by Chantler & Driessens (1995). In agreement with De Roo, I contend that the feathering of the hindlimbs in *Schoutedenapus* may be a first step in the evolution of the Apodine foot. Important evidence is still missing; for example no skeleton has been examined (C. T. Collins, pers. comm.). As it is, I suggest that *Schoutedenapus* should temporarily be included, as an early diverged taxon, in Apodini.

The historical narrative

If the birds, as seems likely (Futuyma 1986, Chiappe 1995; for a good overview, though discordant in conclusions, see Feduccia 1996), evolved from a bipedal running and jumping insectivore catching prey in the air with the mouth (Caple *et al.* 1983), the swifts in principle might be the living representatives of a continuous trajectory, increasingly refining the faculty of flight, all the time using similar food: flying insects. DNA analyses suggest that the hummingbirds diverged from the swifts about 95 million years ago (Sibley & Ahlquist

1990), obviously changing to a different food niche. The earliest records in a revision of fossil swifts (Harrison 1984, see also Feduccia 1996) are from Europe and about 50 million years old.

The swallows have had a shorter time than the swifts for the adaptations to their aerial life. According to DNA analyses (Sibley & Ahlquist 1990) the passerines diverged about 100 million years ago, with the swallows diverging after about half that time. Both swallows and swifts seem to have evolved in and radiated from the Afrotropical region (Brooke 1970b, Turner & Rose 1989). One might have expected a more complex pattern for the swifts, considering their more ancient origin. Perhaps earlier radiations of swifts were largely wiped out in the great extinction about 65 million years ago (not unrealistic, if it was caused by an extraterrestrial impact, Alvarez *et al.* 1980), while one or a few species survived in the Afrotropics, and so had a chance to become ancestral to all later forms.

Winkler & Sheldon (1993) superimposed the nest-building behaviours on a DNA-hybridization phylogeny for 17 species of swallows. A remarkable evolutionary conservatism was revealed. Three main groups are characterised by distinct methods of nest construction. Each method seems to have evolved just once, and the three groups have largely distinct geographical distributions. Those that excavate burrows for breeding are in the Afrotropics, except *Cheramoecca* in Australia, and *Riparia*, which has spread to the northern continents. Those that typically adopt cavities are in the New World, mainly tropical America, except *Psalidoprocne fuliginosa* and *Phedina borbonica* in the Afrotropics. In those that typically build mud nests, *Hirundo* species are spread almost globally, while *Delichon* is restricted to Eurasia. The Tree Martin *Hirundo nigricans* in Australia may seem a cavity adopter, but uses mud on occasions, sometimes building a full mud nest. In contrast to earlier hypotheses (Mayr & Bond 1943, Turner & Rose 1989), burrow excavating was found to be a more primitive state than cavity adoption.

A similar evolutionary conservatism is evident in the five main groups of swifts, which use five distinct substrata for breeding and roosting: (1) the ground, (2) branches of trees, (3) caves, (4) the inside of hollow trees, (5) foliage of trees, holes in trees, crevices in cliffs, etc. Similarly, the five groups have largely distinct geographical distributions.

The first group, the Cypseloidinae, are restricted to the New World, but fossil finds in Europe indicate that they represent an early westward radiation from the Old World. They have an ancient method of nest building, "rooting" living vegetable matter, and so are restricted to humid sites with some daylight near waterfalls (Marín & Stiles 1992, Marín 1997).

In the other groups, probably uniquely in birds, the use of saliva in nest building gave new evolutionary options: to place nests in various dry and/or dark sites.

The treeswifts, in using "the outside" of trees, may seem to have a behaviour with some similarity to that of the Apodine swifts. However, several characters indicate that they diverged much earlier than the

Apodine swifts, even earlier than *Hydrochous*, using branches and not foliage or holes. Their present distribution is in India and eastwards to the Solomon Islands.

In the Collocaliini, *Hydrochous gigas* is similar to the Cypseloidine swifts, nests in daylight near waterfalls (and accordingly has no capability of echolocation), and uses much the same vegetable matter as the Cypseloidine swifts for nest building, but with some saliva mixed in (Somadikarta 1968, Becking 1971). A few Cypseloidine species sometimes nest in dark caves, where they place the eggs on ledges without building a nest (Whitacre 1989). The presence of the tendency towards using caves in some Cypseloidine swifts may strengthen the idea that *Hydrochous* represents an early eastward radiation by Cypseloidine-like swifts, however in an early stage of using saliva in nest building, in the course of time becoming ancestral to the swiftlets. Cypseloidine-like features can be found in some other swiftlets. The Glossy Swiftlet *Collocalia esculenta* cannot echolocate, nests in fairly well lit caves, and uses much vegetable material in its nests (Francis 1987, Chantler & Driessens 1995). Tarburton (pers. comm.) in Western Samoa observed a small colony of the White-rumped Swiftlet *Aerodramus spodiopygius* nesting in the spray of a waterfall in a very light situation on a cliff. Feathering on hindlimbs is present in some Collocaliine species and subspecies (Chantler & Driessens 1995).

The Chaeturine swifts, the spinetails and needletails, all typically use the inside of hollow trees or similar structures, such as chimneys. Their use of the tail as a prop is generally accepted as an explanation for their stiff and square tails with spines. Several genera are present in the Afrotropics; a few of their species are also found far eastwards. The genera *Hirundapus* and *Mearnsia* clearly represent eastward radiations, while *Chaetura*, in the New World, represents a westward radiation.

Most Apodine species are known to use solid sites, like crevices and holes in cliffs or trees, for nesting and roosting. However, I suggest that the original causes for the changes in their hindlimbs (feathering, reduced numbers of phalangi in toes III and IV from 4 and 5 respectively to 3, reorientation of toe I (hindtoe) inwards-forwards, the toes forming a pincer-like grasp, toes I and II opposing toes III and IV, Collins 1983) are linked with use of foliage of trees for nesting (palm swifts, Bock & Miller 1959) and roosting (a behaviour still present, for example, in the Common Swift, Holmgren 1993), and not primarily with clinging to vertical rough surfaces, as has often been claimed. *Schoutedenapus* (with feathered hindlimbs) and the palm swifts (*Aeronautes*, *Panyptila*, *Tachornis*, *Cypsiurus*, with the toes more clearly oriented in opposed pairs than in *Apus* and *Tachymarptis*, which tend towards "all four toes forwards") then may be thought to represent early stages in these changes. I suggest that the Apodine swifts should be characterised by a gradual change in the hindlimbs, in the form of a transformation series, rather than by just the most advanced stages of that change, a redefinition that opens up the possibility to include *Schoutedenapus*. They are present in the

Afrotropics and the Palearctic, but some species spread eastwards, and others westwards to tropical America (*Aeronautes*, *Panyptila*, *Tachornis*).

The hypothetical phylogenetic tree in Figure 1, following this historical narrative, gives a parsimonious solution, and it suggests few changes in the current taxonomy of the swifts (cf. Brooke 1970a, Chantler & Driessens 1995). At present, this only means that it is a simple model for the understanding of swift evolution, and it cannot claim to be faultless.

In the phylogenetic tree there are two cases of convergent evolution. The first one is caused by my insistence on placing the Hemiprocnine swifts together with all other swifts that have one carotid artery and use saliva in nest building. This forces me to admit gradual change towards a narrow sternum and stout humerus in two different lineages. However, that tendency is generally present in the swifts owing to their aerial life style, so this convergence should be expected to be omnipresent in the group, except in the treeswifts.

The second case is the feathering on the legs in some swiftlets, which may be convergent with the earliest stage in the evolution of the Apodine foot.

Comparisons with DNA-analysis phylogenies

In Figure 2 the phylogeny for the swifts presented by Sibley & Ahlquist (1990) is adapted to the earlier proposed standard, so it can be directly compared with the tree in Figure 1. Agreement with Sibley & Ahlquist's results, with *Hemiprocne* in a separate family being the earliest branching, was found in a repeated study using DNA-DNA hybridisation (Bleiweiss *et al.* 1994). The trees in Figures 3 and 4 are adapted from Lee *et al.* (1996), who used DNA-sequencing. They derived the first tree by maximum likelihood estimate based on cytochrome b sequences, the second is a bootstrap consensus tree for 1,000 replicates. Both trees have *Hemiprocne* in the same position as Figure 2. Nevertheless I suggest that this question should be regarded as unresolved, until the new molecular techniques are better understood.

Whether the Cypseloidinae are monophyletic seems to be a question that requires more precision than is attained at present (different results appear in Figures 3 and 4).

The next problem in Figure 2 is the place of *Tachornis*. Convergent change in the hindlimbs in different lineages is certainly possible (cf. the feathering on the legs in some swiftlets). *Aeronautes*, *Panyptila* and *Tachornis* might form a separate tribe, representing an earlier branching than the Apodini. However, that the (reduced) numbers of phalangi in the toes are exactly the same seems to be such a specific character that it strongly suggests monophyly.

Also worrying is the place of *Tachornis* between the needletails and the spinetails. It is possible, but seems unlikely. The place of *Collocalia* nearest to *Apus* then seems very unlikely, since *Hydrochous* so obviously has several characters in common with the Cypseloidine swifts.

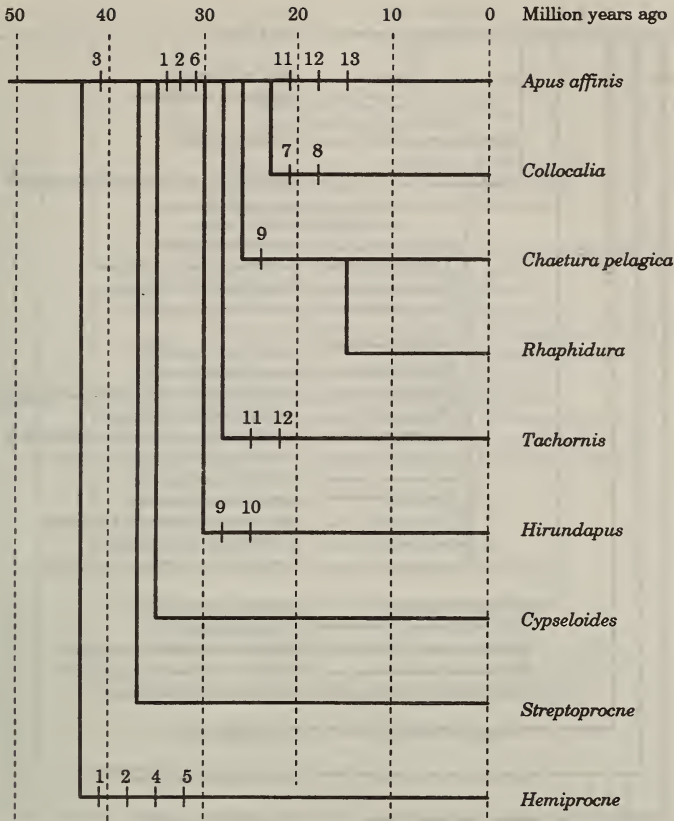


Figure 2. Phylogenetic tree for the swifts, adapted from Sibley & Ahlquist 1990 figure 361, derived by DNA-DNA hybridisation. $\Delta T_{50H} \approx 4.5$ million years. Numbers have same meanings as in Figure 1.

Figures 3 and 4 also have *Hydrochous* near *Apus*. This would force us to infer a very remarkable regression in *Hydrochous*: loss of using caves, loss of echolocation (since it is placed with *Aerodramus*), minimising the use of saliva in nest building, and a renewed use of a behaviour similar to that of the Cypseloidine swifts, nesting near waterfalls and using similar vegetable matter.

A remarkable result in Figures 3 and 4 is the polyphyly of the Collocaliine swifts. In Figure 3, allowing for only a little uncertainty in the applied technique, an arrangement similar to Figure 1, lessening the problem with *Hydrochous*, would appear by connecting the *Collocalia* and the *Aerodramus* branches, leaving *Chaetura* on its own. This also would fit the ectoparasite evidence mentioned by Lee *et al.* (1996). In Figure 4 the situation is far from clear, and seems to reflect difficulties with the applied technique.

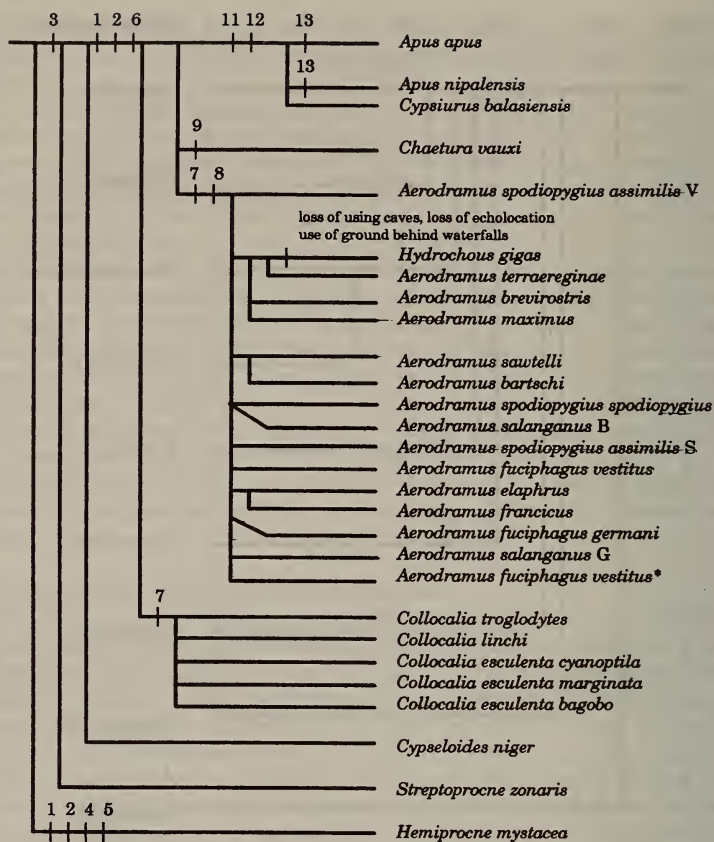


Figure 3. Phylogenetic tree for the swifts, adapted from Lee *et al.* (1996) figure 2, derived by maximum likelihood estimate based on cytochrome b sequences. No time scale. Numbers have same meanings as in Figure 1.

Conclusions

Several studies (Prum 1990, Clayton & Harvey 1993, de Queiroz & Wimberger 1993, Winkler & Sheldon 1993, Paterson *et al.* 1995, Kennedy *et al.* 1996) confirm the opinion that behaviour may be as reliable as other characters for evaluating phylogenies. In the swiftlets, however, Lee *et al.* (1996) did not find nest characters to be phylogenetically reliable. I suggest that behavioural characters in the swifts, at a higher taxonomic level, may reveal an evolutionary conservatism rather similar to that found in the swallows (Winkler & Sheldon 1993).

DNA-hybridization and other techniques for genetic analyses have produced interesting new and independent data for evaluating phylogenies. In the swifts more work is required before consensus may

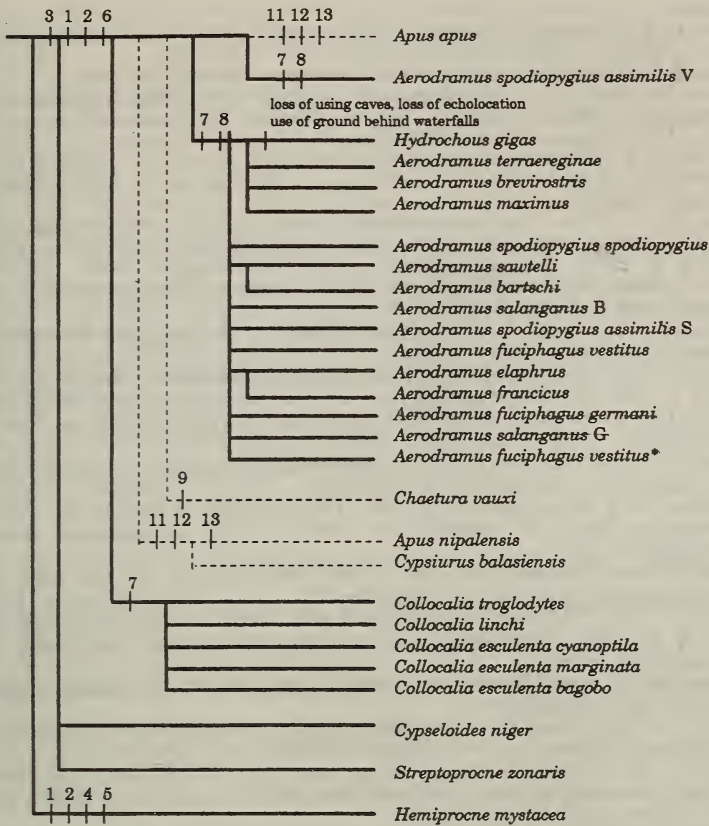


Figure 4. Phylogenetic tree for the swifts, adapted from Lee *et al.* (1996) figure 3, a bootstrap consensus tree for 1000 replicates. No time scale. Numbers have same meanings as in Figure 1.

be established. The aim should be full analyses of all taxa with all available techniques.

Summary

A parsimonious phylogenetic tree for the swifts, which is consistent with a hypothetical historical narrative and zoogeographical facts, is presented. The treeswifts are treated as a tribe Hemiprocnini within Apodinae. Inclusion of the genus *Schoutedenapus* in Apodini is suggested. Three trees based on DNA analyses are adapted in order to facilitate direct comparisons. Differences between the four trees are discussed. Further detailed studies of the swifts with different available techniques are needed.

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